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Sensitivity among species of Solanaceae to AAL toxins produced by *Alternaria alternata* f.sp. *lycopersici*

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The necrotrophic fungus *Alternaria alternata* f.sp. *lycopersici* produces AAL toxins that cause necrosis in tomato tissues with high specificity. Resistance or susceptibility of tomato to the fungus and insensitivity or sensitivity to AAL toxins are determined by a single locus, *Asc*. In order to investigate further the specificity of the host–fungus interaction, 200 species of Solanaceae were tested for their sensitivity to AAL toxins T_A and T_B. Twenty-five species were found to be sensitive to AAL toxins at a concentration of (0·2 μM) used for distinguishing sensitive and insensitive tomato plants. Three species were as sensitive as the sensitive tomato line, indicating that AAL toxins effectively act on a broader range of plant species within the Solanaceae.

Keywords: AAL toxins, *Alternaria*, *Lycopersicon*, necrosis, sensitivity, tomato

Introduction

The necrotrophic fungus *Alternaria alternata* f.sp. *lycopersici*, recently renamed *Alternaria arborescens* (Simmons, 1999), produces host-selective toxins (HST) called AAL toxins, which have a structure similar to fumonisins produced by the unrelated fungus *Fusarium moniliforme*. T_A and T_B are the most active isoforms of AAL toxins (Gilchrist & Grogan, 1976). AAL toxins are analogues of the sphingosine precursor sphinganine, and inhibit ceramide synthase *in vitro* (Gilchrist *et al*., 1995). The disease caused by *A. alternata* f.sp. *lycopersici* in tomato is characterized by dark brown cankers on the stems. The presence of the fungus *A. alternata* f.sp. *lycopersici* has been recorded in Greece (Smith *et al*., 1988) and California, USA (Grogan *et al*., 1975). The foliar symptoms comprise epinasty, inward rolling and angular necrotic spotting of topmost leaflets or, in later stages, complete necrosis of leaflets on one or both sides of the mid-rib (Grogan *et al*., 1975). The fungal conidia first attach to the leaf surface, and germinate by producing a germ tube that attaches to the leaf surface and forms an appressorium which allows penetration of the infecting hypha into the leaf. Resistance or susceptibility to *A. alternata* f.sp. *lycopersici* and sensitivity or insensitivity to AAL toxins in tomato is determined by a single locus, *Asc* (Clouse & Gilchrist, 1987; van der Biezen *et al*., 1995). *In vitro*, ceramide synthases from tomato plants of *Asc*/*Asc* and *asc*/*asc* genotypes are equally sensitive to inhibition by AAL toxins and by fumonisins; therefore inhibition of ceramide synthase appears to be the basis of toxicity, but not the basis of host selectivity (Gilchrist *et al*., 1995). Thus the characterization of this locus may reveal a putative function of the *Asc* product in disease resistance (Mesbah *et al*., 1999). The toxicity of AAL toxins was studied with different tissues of tomato, including leaves, at different stages of plant development. Sensitivity was observed at all levels, the most sensitive tissue being young leaves (Witsenboer *et al*., 1989; Witsenboer, 1991). Toxicity studies with other *Lycopersicon* species (van der Biezen *et al*., 1995) have shown that most are insensitive to AAL toxins at the same concentration used for *Lycopersicon esculentum* (0·2 μM). Only *L. cheesmanii* exhibits the same degree of sensitivity at 0·2 μM as the sensitive *L. esculentum*.

The AAL toxins have been tested as potential herbicides. Most weeds are insensitive to AAL toxins at concentrations up to 5 μM (Abbas *et al*., 1995). Among 100 species tested, only two Solanaceae, jimsonweed (*Datura stramonium*) and black nightshade (*Solanum nigrum*) were sensitive to AAL toxins at a concentration of 5 μM. This confirmed the host-selective character of the AAL toxins within different plant species.

The nightshade family (Solanaceae) is one of the most important families of flowering plants, economically (potato, eggplant, tomato, sweet and chilli peppers), floristically (petunia, angel's trumpet, thorn apple) and

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ethnobotanically (angel's trumpet, belladonna, mandrake) (Olmstead & Palmer, 1992). Members of the Solanaceae also represent good models for genetics (tomato, petunia) and for physiological studies (tobacco). The Solanaceae consists of three subfamilies (Solanoideae, Cestroideae and Nolanoideae), 14 tribes, 96 genera and more than 2000 species (D'Arcy, 1991; Olmstead & Palmer, 1992; Barendse & van der Weerden, 1996). We present here a more extensive study of the sensitivity of solanaceous plants to AAL toxins. New solanaceous genera and species were found to be sensitive to AAL toxins in a leaf bioassay.

Materials and methods

Plant material

Accessions of Solanaceae from the University Botanical Garden of Nijmegen, The Netherlands were grown in the greenhouse or outside, and young leaves were used for experiments (Tables 1 and 2).

The *A. alternata* f.sp. *lycopersici*-susceptible (*asc*/*asc*) Tester-3 (*L. esculentum*) was selected from an F_2 cross between LA1004 and LA1182 (obtained from Dr C. Rick, Tomato Genetics Stock Centre, UC Davis, CA, USA). Near-isogenic paired lines (NIL) of *L. esculentum*, differing with respect to the *Asc* locus, were derived from tomato cultivars Ace 55 VFN (resistant, *Asc*/*Asc*) and Early Pack 7 (susceptible, *asc*/*asc*) by continuous selfing (F_9) of heterozygotes, and were obtained from Dr D. Gilchrist, UC Davis, CA, USA (Clouse & Gilchrist, 1987). Seeds of *L. pennellii* (LA716,G1·1611), *L. cheesmanii*, *L. pimpinellifolium* and *L. hirsutum* were obtained from CPRO-DLO, Wageningen, The Netherlands.

AAL toxins

The isolate of *A. alternata* f.sp. *lycopersici* was subcultured from the original As-27 isolate obtained by D. Gilchrist (Gilchrist & Grogan, 1976).

Cell-free culture filtrate (CFCF) was prepared by growing *A. alternata* f.sp. *lycopersici* containing AAL toxins at 20°C for a week in liquid medium containing potato dextrose agar (PDA) and filtered with Miracloth, Whatman number 1 filter paper, 0·2 μm Minitan plates and 10 000 D Minitan plates. The CFCF stock solution was stored at −20°C (Gilchrist & Grogan, 1976).

Purification of AAL toxins

1 L CFCF was placed on column containing 30 g (25–40 μm) Lichoprep RP-18 (Merck, Darmstadt, Germany) at a speed of 90 mL min^{-1}, and washed with 200 mL demineralized water and 200 mL methanol : water, 40 : 60 (v/v), at a speed of 90 mL h^{-1}. AAL toxins were released by adding 300 mL methanol : water, 55 : 45(v/v), at a speed of 30 mL h^{-1}. Fractions were collected every 4 min and analysed using thin-layer chromatography. Purified AAL toxins contained T_A and T_B. The ratio $T_A : T_B$ was estimated at 4 : 3. Quantification of AAL toxins T_A and T_B was done using mass spectrometry as previously described (Witsenboer, 1991). Dilution of 1 : 100 of the CFCF extract in water corresponded approximately to 0·2 μM AAL toxins.

Leaf bioassay

Young leaflets were cut from the plant to be tested and placed in a 12 cm Petri dish containing filter paper saturated with 3 mL AAL toxins at 0·2 or 0·05 μM purified from CFCF. A water control was added for each accession. The plates with cut leaflets were incubated in a climate cabin under standard conditions (3000 lux of constant light, 25°C) for 72 h before symptoms were assessed.

Seed germination assay

Dry seeds were sown on S&S filter paper saturated with AAL toxins at 0·2 μM containing 3 μM gibberellic acid (GA) to stimulate germination. The effect of AAL toxins on seed germination was estimated after 6 days.

Results

Sensitivity to AAL toxins

It has been shown previously that a leaf bioassay with 0·2 μM purified AAL toxins or1 : 100 diluted CFCF is a convenient method for distinguishing homozygous insensitive tomatoes (*Asc*/*Asc*) from homozygous sensitive (*asc*/*asc*) and heterozygous (*Asc*/*asc*) tomato genotypes (van der Biezen *et al*., 1994). Therefore, AAL toxin sensitivity was defined with sensitive tomato leaves as a reference. Insensitive tomato leaves were indistinguishable from sensitive leaves maintained in water only. Leaves of the homozygous sensitive plants showed a blackening (necrosis) of the lamina, with loss of turgour. The heterozygous tomato leaf showed a visible but less severe necrosis.

In total, 196 species of Solanaceae representing two subfamilies, 13 tribes and 28 genera were tested for sensitivity to AAL toxins in a leaf bioassay with 1 : 100 CFCF (containing 0·2 μM AAL toxins) (Table 1). Twenty-five species or varieties were found to be sensitive to AAL toxins, representing two subfamilies, five tribes and nine genera (Tables 2 and 3). They were then further tested for sensitivity to the purified AAL toxins T_A and T_B. The screening thus covered 66% of subfamilies, 92% of tribes, 29% of genera and 8·5% of species known (Table 1). All species sensitive to AAL toxins belong to the Solanoideae, except *Streptosolen jamesonii* which belongs to the Cestroideae. More than half the sensitive species were members of the genus *Solanum* (Table 3).

Leaf bioassay with 0·2 μM AAL toxins

Out of the 25 accessions (23 species or varieties)

Table 1 Taxonomic disposition of Solanaceae tested for sensitivity to AAL toxins: amount and percentage of tested taxa

Family	Subfamily	Tribe	Genus[a]	Species per tribe[b]	
Tested	2	13	28	196	
Total	3	14	96	2297	
%	66	92	29	8·5	
Solanaceae	Nolanoideae	Nolaneae	None tested	[0]	(22)
	Cestroideae	Anthocercideae	*Duboisia*	[1]	(29)
		Cestreae	*Cestrum*	[9]	(183)
			Cyphomandra		
		Nicotianeae	*Fabiana*	[14]	(210)
			Nicotiana		
			Nierembergia		
			Petunia		
		Salpigossidae	*Browallia*	[9]	(79)
			Brunfelsia		
			*Streptosolen**		
		Schwenckieae	*Schwenckia*	[1]	(79)
	Solanoideae	Datureae	*Brugmansia**	[18]	(18)
			Datura		
		Hyoscyameae	*Hyoscyamus*	[8]	(40)
		Jaboroseae	*Salpichroa*	[1]	(40)
		Juanulloeae	*Juanulloa**	[1]	(40)
		Lycieae	*Lycium*	[1]	(82)
		Solandreae	*Solandra**	[3]	(10)
		Solaneae	*Atropa**	[130]	(1517)
			*Capsicum**		
			*Iochroma**		
			*Lycianthes**		
			Mandragora		
			Physalis		
			*Solanum**		
			Tubocapsicum		
			Withania		
			Witheringia		

[a]Genera including species sensitive to AAL toxins are indicated by asterisks.
[b]Square brackets, number of species actually tested; curved brackets, total number of species known.

sensitive to CFCF, eight, plus two *asc/asc* tomato controls (nos 26 and 27) were tested for their sensitivities to purified AAL toxins T_A and T_B (Table 3). The symptoms observed and the intensity of the reaction were the same for the CFCF and for the purified AAL toxins T_A and T_B. Five species insensitive to AAL toxins and *L. esculentum Asc/Asc* were used as negative controls (nos 28–33). *Lycopersicon esculentum* (*asc/asc*) and *L. esculentum* T3 (*asc/asc*) were used as positive or sensitive controls.

Plant symptoms resulting from AAL toxins exposure were similar to those observed on sensitive tomato leaves: black necrotic spots around the veins. Among the sensitive species, five (four *Solandra* species and *Streptosolen jamesonii*; Table 3) were slightly different from tomato in their responses. Leaves of *Solandra* species lost their turgor first and then became brown. Leaves of *Streptosolen jamesonii* became chlorotic. In total 23 species belonging to nine genera were found to be sensitive to AAL toxins at a concentration of 0·2 μM. Among these 23 sensitive species, five (*Juanulloa aurantica*, *Solandra longiflora*, *Solanum lyratum*, *S. septemlobum*, *S. scabrum*) (Table 3) were as sensitive as tomato (*L. esculentum* near-isogenic lines *asc/asc* and T3). Three of these (*Solanum lyratum*, *S. septemlobum* and *S. scabrum*) were very similar to *L. esculentum* in the severity of symptoms incited at 0·2 μM (Fig. 1). The severity of the symptoms varied among species tested (from completely insensitive 0, to very sensitive, 8). Necrotic symptoms became visible 72 h after toxin exposure in *Solanum lyratum* and *S. septemlobum*, but after 6 days in *Streptosolen jamesonii* and *Solandra* species.

Leaf bioassay with 0·05 μM AAL toxins

A leaf bioassay was performed at a lower dilution of CFCF, equivalent to 0·05 μM AAL toxins, in order to distinguish the degree of sensitivity of the 25 sensitive accessions selected. With the exception of *Solandra* species, the five most sensitive species were sensitive even to 0·05 μM AAL toxins. In total, 10 species sensitive at 0·2 μM AAL were insensitive to 0·05 μM AAL toxins. The sensitivity limits were between 0·2 and

Table 2 Accessions of Solanaceae screened for their sensitivities to AAL toxins

Species	Accession No.[a]
Atropa belladonna	984750098
***Atropa* sp.**	**984750062**
Browallia mexicana	984750130
Brugmansia aurea	924750208
B. aurea	974750040
B. candida cv. Grand Manier	934750212
B. arborea	984750030
B. sanguinea	984750114
B. candida	934750216
B. suaveolens	904750061
B. suaveolens	**974750068**
Brunfelsia americana	814750004
B. calycina	944750006
B. hopeana	894750248
B. hopeana	944750275
B. plicata	924750207
Brunfelsia sp.	814750006
Capsicum chinense	984750047
C. pubescens	984750048
***Capsicum* sp.**	**984750050**
C. calycinum	904750215
Cestrum elegans	804750025
Cestrum sp.	904750240
Cestrum sp.	894750083
Cestrum sp.	934750169
Cestrum sp.	934750172
Cyphomandra. betacea	984750054
C. corymbiflora	944750278
C. endopogon ssp. *guianensis*	974750146
Datura inoxia	984750087
Datura sp. cv. Double Black Currant	984750070
Datura sp.	984750142
Datura sp.	984750143
Datura sp.	984750144
Datura sp.	984750145
Datura sp.	984750147
D. stramonium	984750011
D. stramonium var. *inermis*	984750009
Duboisia leichhardtii	984750103
Dunalia breviflora	904750130
Fabiana imbricata	894750348
Grabowskia duplicata	814750027
Hyoscyamus albus	954750045
H. albus	954750155
H. albus	954750062
H. albus ssp. *major*	894750261
H. albus ssp. *major*	894750335
H. aureus	914750063
H. muticus	974750072
H. pusillus	894750136
Iochroma australe	974750044
I. fuchsioides	944750290
I. grandiflora	944750281
Iochroma sp.	934750223
***Iochroma* sp.**	**984750026**
Juanulloa aurantiaca	**814750028**
Latua pubiflora	944750124
Lycianthes biflora	**830475014**
L. monociniana	**954750013**
L. peduncularis	954750010

Table 2 *continued*

Species	Accession No.[a]
L. rantonnei	814750064
Lycium fremontii var. *congestrum*	904750056
Lycopersicon esculentum	944750232
Nicotiana acaulis	974750092
N. africana	964750014
N. alata	964750113
N. otophora	894750173
N. repanda	894750066
N. rustica	934750197
N. tabacum cv. White Burley	984750038
N. tomentosa	914750067
N. tomentosiformis	914750065
N. trigonophylla	894750176
N. hippomanica var. *violacea*	944750002
Nicotiana sp.	984750031
Petunia sp.	984750061
Physalis alkekengi	984750097
P. coztomatl	934750010
P. coztomatl	934750153
P. fuscomaculata	904750141
P. ixocarpa	984750021
P. ixocarpa	984750074
P. peruviana	984750022
P. peruviana	984750035
P. peruviana	984750056
P. peruviana	984750070
P. peruviana	984750112
P. peruviana	984750090
P. peruviana	984750057
P. pruinosa	984750072
Physalis sp.	984750041
Physalis sp.	984750077
Physalis sp.	984750153
Salpichroa origanifolia	984750094
Schizanthus sp.	984750135
Schwenckia americana	884750248
Solandra grandiflora	**814750035**
S. longiflora	**814750054**
S. maxima	**944750283**
***Solandra* sp.**	**944750289**
Solanum acaule	894750019
S. aculeatissimum	914750001
S. aculeatissimum	904750224
S. aethiopicum	804750136
S. aethiopicum	904750114
S. aethiopicum	914750093
S. aethiopicum	924750076
S. aethiopicum	924750116
S. aethiopicum	934750034
S. aethiopicum	**984750085**
S. aviculare var. *latifolium*	844750003
S. brevidens	924750177
S. brownii	984750120
S. caripense	904750133
S. cervantesii	**814750013**
S. cervantesii	**814750041**
S. codonanthum	904750178
S. crinitum	934750219
S. cyaneopurpureum	914750102
S. depilatum	904750062
S. discolor	824750025
S. dulcamara	974750113

Table 2 *continued*

Species	Accession No.[a]
S. dulcamara var. *marinum*	854750003
S. dulcamara var. *littorale*	884750057
S. dulcamara	904750012
S. dulcamara **var.** ***maritima***	**884750088**
S. dulcamara var. *littorale*	914750081
S. fraxinifolium	904750201
S. heterodoxum	924750172
S. incanum	904750229
S. incanum	924750118
S. incanum	904750046
S. linnaeanum	934750014
S. linnaeanum	884750074
S. luteoalbum	904750266
S. lyratum	**914750106**
S. macrocarpon	874750022
S. mammosum	924750111
S. mauritianum	934750157
S. melongena	914750091
S. melongena	884750026
S. melongena	984750059
S. microdontum	804750174
S. muricatum	964750119
S. myriacanthum	814750043
S. nigrescens	**944750261**
S. nigrum	984750019
S. nummularium	984750119
S. palitans	904750206
S. pennellii	974750069
S. pennellii var. *puberulum*	914750050
S. platense	814750061
S. pseudocapsicum var. *diflorum*	804750131
S. pseudocapsicum **var.** ***diflorum***	**804750133**
S. pseudocapsicum var.*diflorum*	934750100
S. pseudocapsicum **var.** ***pseudocapsicum***	**934750191**
S. pseudocapsicum **var.** ***pseudocapsicum***	**874750034**
S. scabrum	**924750073**
S. scabrum	**944750242**
S. scabrum	944750239
S. septemlobum **var.** ***indatum***	**934750192**
S. sisymbriifolium	974750116
S. sisymbriifolium	944750123
S. smithii	**964750135**
S. sodomaeum	984750018
Solanum sp.	894750089
Solanum sp.	904750239
Solanum sp.	904750285
Solanum sp.	924750097
Solanum sp.	954750418
Solanum sp.	974750022
Solanum sp.	974750025
Solanum **sp.**	**884750134**
S. tabanoense	984750001
S. tripartitum	884750218
S. uporo	924750005
S. vespertilio	934750021
S. violaceum	874750016
Streptosolen jamesonii	**934750165**
Tubocapsicum anomalum	914750107
Withania adpressa	874750015
W. aristata	874750014
W. coagulans	914750053
W. somnifera	904750143
W. somnifera	934750118
Withania sp.	894750198
Withania sp.	894750225
Withania sp.	914750115
Witheringia coccoloboides	814750081
W. solanacea	814750082

[a]Accessions sensitive to 0·2 μM AAL toxins are indicated in bold.

0·05 μM for these 10 species (Table 3). The results were essentially the same with purified AAL toxins and with CFCF.

Germination test with AAL toxins

Seeds of some accessions were tested for germination on filter paper saturated with 1 : 100 CFCF. Results showed that seedling sensitivities to AAL toxins corresponded to those of the leaves except in two cases: seedlings of *Solanum dulcamara* were sensitive whereas leaves were insensitive. Surprisingly, *S. lyratum* did not show any sensitivity in the seed germination test, although leaves were highly sensitive to AAL toxins.

Discussion

Sensitivity to AAL toxins

Leaves of 196 species of Solanaceae were tested for sensitivity to AAL toxins. For most of the 23 species or varieties sensitive to 0·2 μM AAL toxins, the symptoms observed on leaves were similar to those observed in tomato, i.e. black necrotic spots between and along the veins, with a loss of turgour. Essentially, the same responses were observed with either CFCF (1 : 100) or with purified AAL (a mixture of T_A and T_B isoforms).

Five species (four *Solandra* spp. and *Streptosolen jamesonii*; Table 3) sensitive to AAL toxins showed slightly different symptoms from those observed in tomato. The target of AAL toxins could be different for these plants with different responses. Alternatively, AAL toxins may have the same target with a similar mechanism, but leading to different symptoms. In that case the difference in symptoms observed could be due to a structural difference in the leaf tissue.

Using AAL toxin concentrations of 0·2 μM and even 0·05 μM, we demonstrated that AAL toxins are specific not only to the (*asc*/*asc*) tomato isolines, but also to other species of Solanaceae. These results show that the selectivity potential of the AAL toxins is not absolute. AAL toxins currently described as HST were shown here not to be restricted to the hosts of the producer. The same question could be raised for other HST toxins regarding their plant range selectivity (Walton & Panaccione, 1993; van der Biezen *et al*., 1994; Walton,

Table 3 Sensitivity of accessions of Solanaceae to AAL toxins supplied as cell-free culture filtrate (CFCF) or purified T_A and T_B isoforms, in two concentrations

Species	Accession number	CFCF (equivalent to μM AAL) 0·2 (leaves)	0·05 (leaves)	0·2 (seeds)	Purified AAL toxins (T_A and T_B in μM) 0·02 (leaves)	0·05 (leaves)
1 *Atropa* sp.	984750062	4	0	2	–	–
2 *Brugmansia suaveolens*	974750068	3	0	–	4	4
3 *Capsicum* sp.	984750050	5	0	2	–	–
4 *Iochroma* sp.	984750026	5	4	–	3	2
5 *Juanulloa aurantiaca*	814750028	6	4	–	–	–
6 *Lycianthes biflora*	830475014	3	0	5	–	–
7 *L. monociniana*	954750013	5	4	–	5	4
8 *Solandra grandiflora*	814750035	5	0	–	–	–
9 *S. longiflora*	814750054	6	0	–	6	0
10 *S. maxima*	944750283	4	0	–	4	0
11 *Solandra* sp.	944750289	3	3	–	4	0
12 *Solanum aethiopicum*	984750085	3	2	–	–	–
13 *S. cervantesii*	814750013	4	3	1	3	0
14 *S. cervantesii*	814750041	3	2	3	–	–
15 *S. dulcamara*	884750088	3	2	6	–	–
16 *S. lyratum*	914750106	8	7	0	–	–
17 *S. nigrescens*	944750261	4	2	3	–	–
18 *S. pseudocapsicum* var . *pseudocapsicum*	874750034	4	0	6	–	–
19 *S. pseudocapsicum* var . *diflorum*	804750133	3	2	4	–	–
20 *S. septemlobum*	934750192	7	6	7	–	–
21 *S. smithii*	964750135	2	1	–	–	–
22 *Solanum* sp.	884750134	4	3	6	–	–
23 *S. scabrum*	944750242	4	0	4	–	–
24 *S. scabrum*	924750073	6	5	5	–	–
25 *Streptosolen jamesonii*	934750165	4	0	–	4	0
26 *Lycopersicon esculentum*	T3	6	4	6	4	4
26 *Lycopersicon esculentum (asc/asc)*	5	4	–	4	4	
27 *L. esculentum (asc/asc)*		0	0	0	0	0
28 *L. esculentum Asc/Asc*		0	0	–	0	0
29 *L. pennellii*	LA716	0	0	–	–	–
30 *Nicotiana glauca*	924750158	0	0	–	–	–
31 *Physalis peruviana*	984750035	5	4	–	4	4
32 *Solanum depilatum*	914750062	0	0	–	–	–
33 *S. melongena*	884750026	0	0	0	0	0

Symptom severity scale ranges from 0 (no symptoms visible) to 10 (complete necrosis of tissue).

1996). Germination tests with 0·2 μM AAL toxins showed that with two exceptions, plants whose leaves are sensitive to AAL toxins also have sensitive roots. Differences between root and leaf sensitivity to AAL toxins have been shown previously in tomato (Witsenboer *et al*., 1989; van der Biezen *et al*., 1996).

Among the solanaceous species tested, almost half those plants sensitive to AAL toxins belong to the genus *Solanum* (14 out of 25). This could be explained by the high proportion of *Solanum* species tested (130 out of 200). Another explanation is that the genus *Solanum* is a close relative of the genus *Lycopersicon*.

Three species, *Solanum lyratum*, *S. septemlobum* and *S. scabrum*, were as sensitive as, and exhibited similar symptoms to, *L. esculentum* (*asc/asc*). A comparison of the *Asc* gene for these accessions would be interesting at the genetic and molecular levels.

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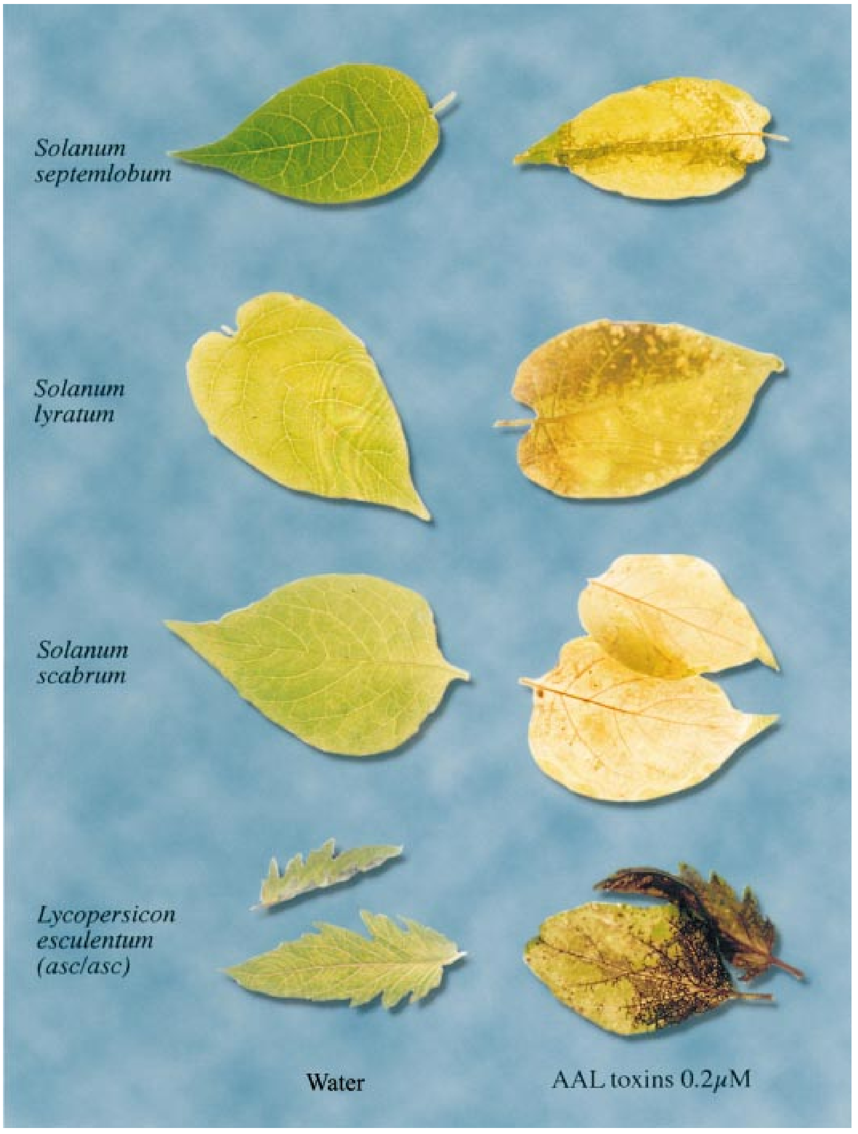

Figure 1 Leaves of four different species of Solanaceae sensitive to 0·2 μm AAL toxins. *Lycopersicon esculentum* is used as a positive control.

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